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Factors Influencing Year-Class Strength of Percids: A Summary and a Model of Temperature Effects[1]

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KOONCE, J. F., T. B. BAGENAL, R. F. CARLINE, K. E. F. HOKANSON, AND M. NAGIĘĆ. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. J. Fish. Res. Board Can. 34: 1900–1909.

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Key words: Percidae, year-class strength, temperature, probalistic model, early life history

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Nous résumons les facteurs contrôlant l'abondance des classes d'âge des genres de percidés *Stizostedion* et *Perca*. Dans plusieurs plans d'eau, il y a corrélation significative entre un indice du régime des températures de l'eau et l'abondance des classes d'âge de percidés. On note une synthconie modérée dans l'abondance des classes d'âge du doré jaune (*Stizostedion vitreum vitreum*) dans plusieurs lacs nords-américains. Nous proposons un modèle probabiliste pour expliquer comment l'abondance des classes d'âge des percidés dépend de la température. Mais des essais du modèle avec des données du lac Erié indiquent que les corrélations observées entre la température et l'abondance des classes d'âge tant de perchaudes (*Perca flavescens*) que de dorés jaunes peuvent ne pas être le résultat d'effets directs du régime de températures sur la survie au début du cycle biologique.

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IN this paper we summarize the major factors thought to regulate year-class strength in the genera *Stizostedion* and *Perca*. We also report a tentative pattern of year-class synchrony in North America and advance a model based on the temperature dependence of mortality in early life history to explain variation in the year-class strength of species in these two genera.

Contributions to the PERCIS Symposium revealed the universality of fluctuations in year-class strength in populations of species in the two

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genera. The phenomenon was mentioned in at least 23 of the papers presented, which represented water bodies varying in area, depth, flushing rate, intensity of exploitation, and the species composition of associated fishes. For the Eurasian species, the range of the fluctuation was greater for Eurasian perch (*Perca fluviatilis*) than for pikeperch (*Stizostedion lucioperca*). In Lake IJssel, for example, Willemsen (1977) reported that the ratio of the strongest to weakest year-class was 100 for perch and 20 for pikeperch. Kipling (1976) reported a large (400-fold) variation in perch year-class strength in Lake Windermere and year-class strength fluctuations of pikeperch have been observed to range from 10-fold to 55-fold in other European water bodies (Boiko 1964; Lind 1977; and Rundberg 1977). In North America, yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) have similar patterns of fluctuation of year-class strength. Yellow perch year-class strength has been reported to vary from 8-fold to 40-fold (Forney 1976; Smith 1977; Eshenroder 1977; Nelson and Walburg 1977). Walleye, in comparison, is reported to have year-class strength fluctuations of 12-fold–74-fold (Spangler et al. 1977; Smith 1977; Forney 1976; Carlander 1977; Kempinger and Carline 1977; Nelson and Walburg 1977; Busch et al. 1975). In some lakes yellow perch seem to have a greater variation in year-class strength than walleye (Forney 1976; Smith 1977), but the pattern is reversed elsewhere (Leach and Nepszy 1976).

Attempts to analyze the patterns of fluctuation ultimately are limited by the variation in methods of estimating year-class strength. Methods used include year-class contribution to a fishery, catch per unit effort for reference gears, mark-and-recapture technique, and trawl catches of year 0 juveniles. Not all of these methods yield the same estimates of year-class strength (e.g. Forney 1976). Thus, the comparison between water bodies of the amplitude of fluctuation in year-class strength of any species is limited. Nevertheless, the year-class strength of these fishes appears to be fixed either by the year 0 juvenile stage (Busch et al. 1975; Willemsen 1977) or by midsummer of the 2nd yr, year 1 juveniles (Forney 1976).

Factors Associated with Year-Class Strength

Various factors have been associated with the determination of year-class strength in percids. The most important physical factors appear to be water temperature, wind, and water level of lakes or flow rate of rivers. Less often, reports mention water transparency, oxygen concentration, and siltation of spawning grounds. Biotic factors include predation, cannibalism, prey availability, and size of spawning stock or stocking intensity. Although all of these factors may be interrelated, the water temperature regime may affect mortality rates directly or indirectly through any of the other factors and may thus be an ultimate cause of variation in year-class strength for many water bodies.

Most studies we reviewed implicated water temperature as a dominant factor regulating year-class strength. Using a variety of measures of the temperature regime, many authors found a positive correlation between water temperatures and survivorship of one or more development phases. Busch et al. (1975) found strong correlations between rates of spring warming and both total egg production and fry densities for a 10-yr period in Lake Erie. Eshenroder (1977) reported a similar relationship for yellow perch in Saginaw Bay for a 24-yr period. Nagięć (1977) reported the highest correlation between mean monthly temperature during spawning and incubation and the abundance of pikeperch year-classes. Positive correlations between air temperature and year-class strength were also reported (Svardson and Molin 1973), but other attempts to find correlations with air temperature have not produced significant relationships (Doan 1942; Jobes 1952; El-Zarka 1959; Heyerdahl and Smith 1971).

Apart from these attempts to find correlations, some studies showed the climatic regime to act on year-class strength in a discontinuous manner. Periods of cold weather, for example, seem to be associated with weak year-classes (Derback 1947; Smith and Krefting 1953; Walburg 1972). Bagenal (1977) and Kipling (1976) showed that weak year-classes of perch in Lake Windermere are always associated with cold summers (<150 degree-days above 14°C). Other authors noted that warm summers seem to produce strong year-classes (Payne 1964; Kuznetsov 1970). Only three studies in the PERCIS Symposium indicated lack of any relationship with water temperature (Carlander and Payne 1977; Kempinger and Carline 1977; Willemsen 1977).

The importance of the other physical factors (wind, water level, and flow rate) appeared to be less general. Mean daily wind velocity accounts for much of the variation in survival of early stages of yellow perch in Oneida Lake (Clady 1976), but in other studies wind does not correlate significantly with strength of year-class (Busch et al. 1975). For river spawning populations of walleye, Spangler et al. (1977) reported a positive relationship between flow rate and strength of year-class. A positive association between water level and year-class strength in walleye and pikeperch has also been reported for

several water bodies: reservoirs on the Missouri River (Nelson and Walburg 1977); reservoir of Kaunas, Lithuania (Virbickas et al. 1974); Rainy Lake, Ontario, which has water level regulated by a dam (Chevalier 1977); the delta of the Neman River in Lithuania (Virbickas et al. 1974); lakes with substantial marshes (Clear Lake, Iowa, Carlander and Payne 1977; Lake Winnebago, Wisconsin, Priegel 1970); and some Swedish lakes (Svardson and Molin 1973).

Analysis of biotic factors regulating year-class strength is complicated by the predator–prey relationships for *Stizostedion* and *Perca* species. All species of these two genera are both potential predators as well as potential prey. As adults, they prey on several fish species, if available, and they shift readily to cannibalism. They are especially vulnerable to predation in the 1st yr of life. Forney (1977) concluded that prey availability regulates both growth of adult walleye and walleye year-class strength in Oneida Lake. Willemsen (1977) observed an analogous relationship between smelt and pikeperch in Lake IJssel. These studies imply a possible self-regulation mechanism for percid populations. In some unexploited populations of salmonids, large standing stocks of adults suppress recruitment (Johnson 1976). A similar regulation method has been observed in ponds in which perch is the only fish species (Alm 1951; Menshutkin and Zhakov 1964; Sumari 1971). In these cases, a single year-class predominates and other strong year-classes only occur when the density of the dominant year-class drops to some low level.

Prey availability may also influence year-class strength. The most critical aspect of food availability seems to be the timing of specific preferred food (Menshutkin et al. 1968; Momot et al. 1977; Nagięć 1977; Willemsen 1977). Hokanson (1977) showed food density to be important to initiation of feeding and survival of pelagic larvae of yellow perch. In studies of competitive interaction, Johnson and Hale (1977) reported a 15-fold increase in yearling yellow perch and walleye following white sucker (*Catostomus commersoni*) removal from Wilson Lake, Minnesota. Johnson (1977) observed a decrease in walleye density with increasing density of smallmouth bass (*Micropterus dolomieui*).

Stock–recruitment relationship are not obvious for these percids. Some observations indicated a positive relationship between brood-stock density and year-class strength (Chevalier 1977; Busch et al. 1975; Shuter and Koonce 1977). But others found either no relationship or a negative one (Willemsen 1977; Smith 1977; Schneider and Leach 1977; Eshenroder 1977; Bagenal 1977).

Generality of Year-Class Strengths

From the assembled expertise at the PERCIS Symposium we attempted to find a pattern of year-class strengths common to various lakes. Because of the major importance of water temperature, we reasoned that climatic effects might show some consistency within certain geographical areas. We polled individuals to determine the years in which strong year-classes of any percid species were observed in the water bodies for which they had data. We obtained these estimates (Table 1) for 10 European lakes and 18 lakes and bays of large lakes in North America. Among the North American lakes, we observed a moderate synchrony. At least 20% of the lakes represented had strong year-classes of walleye in 1954, 1959, 1962, 1965, and 1972. The appearance of this synchrony is noteworthy, but the kind of information we acquired needs more careful review. In retrospect, we should have also surveyed weak year-class timing. Nevertheless, the data we have suggest some underlying trends, which were also noted by Eshenroder (1977), and should be developed more rigorously in future work.

Probabilistic Model of Year-Class Strength in Percids

Factors associated with year-class strength may be applied in a probabilistic manner to a sequence of development phases (Fig. 1). To use this conceptual model, we evaluated the direct effects of water temperature on survivorship of early life-history stages of yellow perch. Other factors such as food availability, predation, and cannibalism, which are also temperature dependent, may modify these survival probabilities, but insufficient data exist to evaluate their regulatory role with this model. The following discussion presents the assumptions and data used to construct a model from the concepts in Fig. 1.

Spawning and maturation — Hokanson (1977) summarized information available on the role of temperature in the production of viable eggs. Spawning temperature is a complicated function of an organism's temperature history. To initiate the model, therefore, we assumed a stock-specific optimum spawning temperature of 5°C. Time of spawning is estimated from a temperature record for a specific lake, and viability is assumed to be 60%.

Probability of surviving cleavage-egg phase — The time required to complete this phase is a function of incubation temperature (Hokanson 1977). However, temperature of incubation also

TABLE 1. Years during 1940–76 in which strong year-classes of percids[a] were reported in the PERCIS Symposium for various European and North American Lakes. Within each group, lakes are listed in order of increasing latitude.

	Year																																		
	1940										1950										1960										1970						
Lake	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
European lakes																																					
Baalton													0								0				0				0								
Constance																												X				X		X		
Klivaca																					X	X					X										
IJssel		0				0		0	0		0																			0,X	X	X		0,X	X	0,X	0,X
Jesiorak														0														0		0			0				
Windermere		X			X					X						X					X																
Loch Leven																									X				X			X					
Hjälmaren														0							0						0			0						0	
Mälaren														0		0					0						0	0		0							
Kolliolamni																												X									
North American lakes																																					
Norris Res.																														W							
Erie															W		W				W			W			W			W		W		W			
St. Clair															W		W				W			W			W			W		W		W			
Clear Lake									W	W	W	W															W			W		W					
Bay of Quinte														W				W			W																
Oneida														W				W			W	W		W		W			W	W		W					
Huron																					W			W		W				W						W	
Georgian Bay																W					W	W				W											
Winnebago																					W																
Pike Lake																					W																
Green Bay				W						W	W	W																		W			W	W			
Oahe																																					
Escanaba																					W		W			W											
Mille Lacs															W						W																
Leech																								W		W											
Red-Lakes						W	W						W		W																						
Lake of the Woods																								W		W											

[a]X, *Perca fluviatilis*; 0, *Stizostedion leucioperca*; W, *Stizostedion vitreum vitreum*.

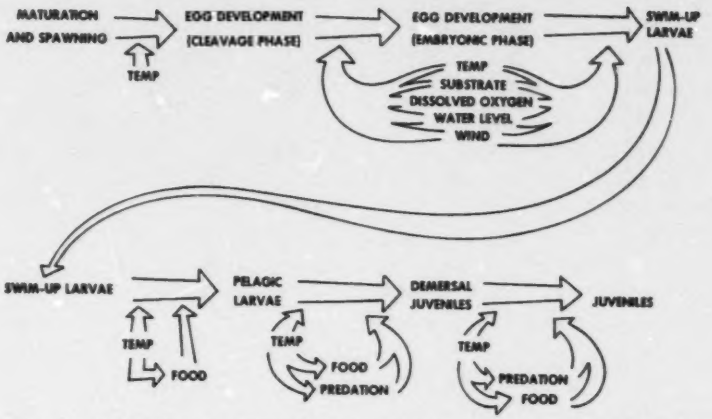

FIG. 1. Interactions of factors that determine year-class strength of *Perca* and *Stizostedion* species.

affects survival (Hokanson and Kleiner 1974). Using these two relationships, we relate the probability of survival through this stage by

$$(1)\quad P_1 = 1 - \sum_{i=1}^{n} {}^1D_i$$

where n is the number of days required to complete the phase and ${}^1D_i$ is the temperature-dependent death rate calculated from Hokanson (1977). Because the time required to complete the phase is temperature dependent, we had to assume a daily rate of development, which is also temperature dependent. On a rising temperature regime, we considered the phase completed when the cumulative development equals or exceeds a value of 1.0. Temperature dependence of mortality rate is given in Table 2, and development rates at various temperatures are

	Development rate (day^{-1})	
Temp (°C)	Cleavage egg	Embryo
3	0.071	0.028
6	0.154	0.028
9	0.283	0.043
12	0.444	0.075
15	0.611	0.125
18	1	0.154
21	1	0.2
24	1	0.2
27	1	0.2
30	1	0.2

Probability of surviving the embryonic phase — We calculated survival of this phase in a manner similar to that for the cleavage-egg phase.

TABLE 2. Daily mortality rates for phases of yellow perch from cleavage egg to swim-up larvae

Temp (°C)	Cleavage egg	Embryo	Swim-up larvae
3	0.050	0.027	1.0
6	0.005	0.018	0.85
9	0.003	0.018	0.42
12	0.000	0.015	0.12
15	0.050	0.019	0.02
18	0.160	0.008	0.0
21	0.70	0.020	0.08
24	1.0	0.150	0.20
27	1.0	0.2	0.45
30	1.0	0.2	1.0

Again using the data of Hokanson and Kleiner (1974) we implement the following function:

$$(2)\quad P_2 = 1 - \sum_{i=1}^{n} {}^2D_i$$

where n is the number of days required to complete the phase and ${}^2D_i$ is the temperature-dependent death rate. Development rates and death rates were computed from Hokanson (1977) as described above. Values for development rates are summarized above and mortality rates are given in Table 2.

Probability of surviving swim-up phase — The swim-up phase corresponds to the eleutheroembryonic phase described by Balon (1975). We treated the temperature dependence of survival in the same way as for egg development. Hokanson (1977) reported that development times for this phase were approximately 1 day

and that survival was temperature dependent. We thus defined survival probability for this phase as

$$(3)\quad P_3 = 1 - {}^3D_i$$

where ${}^3D_i$ is the daily death rate (Table 2).

Probability of surviving pelagic larvae phase — We assumed that an individual larva starts this phase at some weight and continues in the pelagic phase until a minimum weight is achieved. The growth relationship is

$$(4)\quad B_t = B_0 e^{k g_m t}$$

where B_t is the weight per individual at time t, B_0 is the starting weight, k is the temperature-dependent fraction of maximum growth rate, and g_m is the maximum growth rate. The value of k depends on consumption and temperature in a manner similar to that developed by Kitchell et al. (1974, 1977):

$$(5)\quad k = pr_c - r_R$$

where p is a coefficient related to the availability of prey, and r_c and r_R are functions of temperature described by Kitchell et al. (1977). Parameter values are given in Table 3. We then estimate survival of the phase by

$$(6)\quad P_4 = e^{-\sum_{i=1}^{t_m} {}^4D_i}$$

where ${}^4D_i$ is the temperature-dependent death rate and t_m is the time required to complete the phase. The instantaneous daily mortality coefficients for various temperatures were calculated from McCormick (1976):

Temp (°C)	Instantaneous mortality (day^{-1})
3	0.0002
6	0.0002
9	0.0010
12	0.0058
15	0.0050
18	0.0030
21	0.0030
24	0.0040
27	0.0004
30	0.0002

Unfortunately, these mortality coefficients were obtained for juvenile yellow perch. We suspect the pelagic larvae to be more stenothermic, but no data are available to obtain more suitable parameters for the model.

Probability of surviving demersal juvenile phase — Fish in this phase have completed larval development and move from a pelagic to a demersal habitat. In our simulations we assumed that fish remain in this phase for the rest of the year to day 360. We also assumed that mortality during this phase depended on temperature, and the probability of survival was determined by

$$(7)\quad P_5 = e^{-(\alpha t_m + \sum_{i=1}^{t_m} {}^5D_i)}$$

where ${}^5D_i$ is the same temperature-dependent death rate used for the pelagic larvae and α is the base natural mortality, which we assumed to be 0.017·day^{-1}.

The relative year-class strength, or joint-survival probability, was calculated

$$(8)\quad P = P_1 \cdot P_2 \cdot P_3 \cdot P_4 \cdot P_5 \cdot 0.6$$

Actual year-class strength could be calculated from estimates of the density and fecundity of the brood stock. As a test of the model calibration, we compared (Fig. 2) the survival probabilities of the three early development phases of yellow perch with the experimental data of Hokanson and Kleiner (1974). The good agreement then allowed us to test the model on a variable temperature case.

TABLE 3. Parameter values for larval growth in equations 4 and 5. Both r_c and r_R are temperature dependent functions described by Kitchell *et al.* (1977).

Parameter	Value
g_m	0.052·day^{-1}
B_0	1.0 mg/ind
B_m	150.0 mg/ind
p	1.0[a]
	r_c constants
T_m	32.0°C
T_0	23.0°C
Q_{10}	2.3[a]
	r_R constants
R_m	0.14[a]
T_m	35.0°C
T_0	28.0°C
Q_{10}	2.1[a]

[a]Dimensionless constant.

Application of Model to Perch and Walleye in Lake Erie

We chose to test the model by comparing observed and predicted year-class strengths of perch and walleye in Lake Erie. Three factors

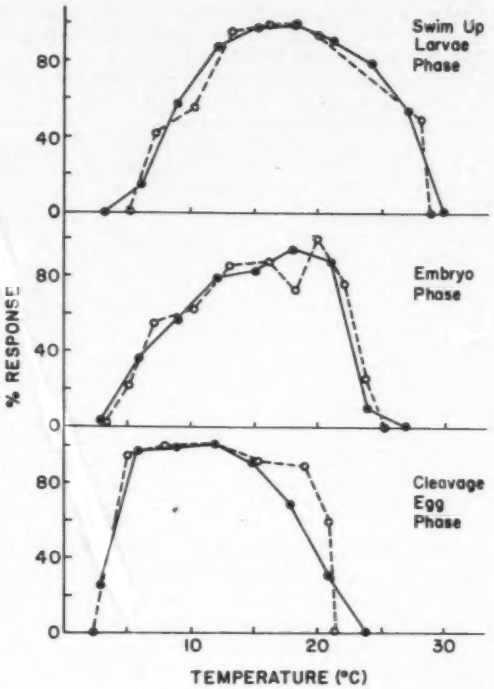

FIG. 2. Comparison of survival probabilities of early development phases of yellow perch predicted by model (●) and observed by Hokanson and Kleiner (1974) (○).

motivated this choice. First, year-class strength of walleye in the western basin of Lake Erie over the period of 1959–70 had a significant correlation to the temperature regime in the spring (Busch et al. 1975), and a similar relationship seemed to hold for perch (Hartman 1972). Second, daily temperatures of surface waters at South Bass Island were available for the period 1918–76 from the Ohio Department of Natural Resources (1961; and unpublished data). Third, the walleye and yellow perch populations in Lake Erie were highly exploited during this period. Under this condition we would expect recruitment to be most sensitive to climatic fluctuations. The application of this model for yellow perch and walleye assumed that the two species have the same physiological dependence on temperature. Although Hokanson (1977) suggested that walleye may be a few degrees less tolerant than yellow perch, Kitchell et al. (1977) were successful in describing temperature dependence of walleye growth using parameters derived for perch. Thus, given the similarity in their ranges and life history we considered that this assumption was not unreasonable.

Predicted survival of the early life-history stages of both yellow perch and walleye did not agree with the observed patterns of year-class strength in the western basin of Lake Erie. The joint-survival probability for 1959–70 had a relatively narrow range, 0.087 in 1967 to 0.132 in 1960 (Table 4), which contrasts with the 74-fold range for walleye and 18-fold range for yellow perch (Table 5). Using a nonparametric measure of rank correlation (Spearman r_s, Conover 1971), no significant correlation could be detected between predicted survival and observed year-class strength of either yellow perch or walleye, but

TABLE 4. Predicted survival probabilities of various life-history stages of yellow perch and the joint-survival probability (P) of the early life history from egg fertilization through age 0 juveniles, 1960–70. Life-history intervals reported are cleavage egg (P_1), embryo (P_2), swim-up larvae (P_3), pelagic larvae (P_4), and age-0 juvenile (P_5).

Year	P_1	P_2	P_3	P_4	P_5	P
1960	0.971	0.695	0.895	0.997	0.366	0.132
1961	0.979	0.654	0.922	0.997	0.370	0.131
1962	0.972	0.640	0.911	0.996	0.347	0.118
1963	0.963	0.619	0.847	0.996	0.335	0.101
1964	0.954	0.639	0.924	0.996	0.334	0.112
1965	0.953	0.692	0.917	0.996	0.343	0.124
1966	0.903	0.614	0.815	0.999	0.350	0.095
1967	0.971	0.572	0.736	0.997	0.354	0.087
1968	0.974	0.715	0.906	0.997	0.341	0.129
1969	0.970	0.601	0.870	0.997	0.376	0.114
1970	0.972	0.660	0.901	0.997	0.331	0.114

TABLE 5. Rates of spring warming and indices of year-class strength in walleye and yellow perch of western Lake Erie, 1960–70.

Year	Rate of warming (°C/day)[a]	Walleye[b]	Perch[c]
1960	0.18	0.4	420
1961	0.24	7.8	1300
1962	0.29	29.6	2800
1963	0.20	1.5	210
1964	0.32	11.0	330
1965	0.36	11.1	2300
1966	0.10	0.6	160
1967	0.13	3.4	340
1968	0.12	1.7	160
1969	0.24	5.2	180
1970	0.31	28.2	640

[a]Mean daily rate of temperature increase from April to mid-May (Busch et al. 1975).

[b]Number of young-of-the-year walleye caught per hour of trawling (from Busch et al. 1975).

[c]Number of young-of-the-year perch caught per hour of trawling (from Leach and Nepszy 1976).

significant correlations are found for rate of spring warming and both walleye and yellow perch year-class strength and for walleye year-class strength and yellow perch year-class strength:

Comparison	Correlation coefficient r_s	P
Predicted survival vs. walleye YCS	0.091	>0.1
Predicted survival vs. yellow perch YCS	0.382	>0.1
Walleye YCS vs. yellow perch YCS	0.664	<0.025
Rate of warming vs. walleye YCS	0.841	<0.001
Rate of warming vs. yellow perch YCS	0.682	<0.025

The correlation between rate of spring warming and walleye year-class strength is consistent with the observations by Busch et al. (1975).

Although the predicted survival probabilities did not correlate significantly with observed walleye year-class strength, predictions of the timing of the hatch were much better. Predicted hatching of walleye (swim-up phase) occurred over a range of April 27–May 15, and the observed range of midhatching for the same period was May 1–12 (Busch et al. 1975):

Year	Observed date of midhatching	Predicted date of hatching
1960	May 10	May 8
1961	May 12	May 15
1962	May 4	May 4
1963	May 3	May 1
1964	May 7	May 9
1965	May 11	May 11
1966	May 8	May 4
1967	May 8	May 1
1968	May 1	April 27
1969	May 6	May 5
1970	May 11	May 5

Thus, the temperature dependence of development seemed to be more accurately described than survivorship.

Discussion

Our simulation results indicate that direct temperature effects on mortality of various early life-history phases of perch and walleye may not determine the year-class strength in western Lake Erie. Although the model accounts for about 90% of the mortality as due to temperature dependence of mortality, the narrow range of the joint-survival probability and the absence of any significant correlation of joint-survival probability to observed year-class strength argue against a regulatory role for the temperature regime. In fact, the relatively high survival probabilities through the pelagic larvae phase may indicate that the temperature regime in western Lake Erie is nearly optimal for normal development of perch and walleye.

A significant correlation between year-class strength of these fishes and temperature regime could result from climatic influences on other aspects of population regulation. Spawning behavior, for example, may be affected by the weather conditions during a 2-wk period in the spring. Busch et al. (1975) reported significant correlations between rate of warming and both egg deposition and year 0 juvenile density, which is a good predictor of year-class strength. Rank correlation of year-class strengths indicated by egg deposition and year 0 juvenile density is significant ($r_s = 0.64$, $P < 0.025$). Thus the relative year-class strength in Lake Erie appears to be fixed before our simulations started.

Our results, therefore, suggest that temperature may limit year-class strength directly only under severe climatic regimes. These regimes occur with greatest frequency at the northern and southern boundaries of the ranges of these percid species, but may also occur periodically elsewhere (cf. Kipling 1976). The model might be used to explore range limitation or to determine possible effects of thermal stress. The occurrence of significant correlations between year-class strength and temperature in the middles of the ranges of these species, however, cannot be explained by the model we formulated. Spawning behavior, availability of specific types of food at various critical phases of development, predation and cannibalism rates, mortality of adults, and various abiotic factors may also have some correlation with temperature or act synergically with the physiological effects of temperature. Temperature effects on growth rate (e.g. Kitchell et al. 1977), for example, may prolong exposure to some other mortality factor.

Many of these interactions might be evaluated with the type of model developed here. For instance, joint effects of temperature and food density on growth and survival probabilities of larval percids could be incorporated by using some bio-energetic model (e.g. Brett et al. 1969; Kitchell et al. 1974; Kitchell et al. 1977). Inclusion of predation models that relate survival probabilities to development phase, temperature, alternative prey densities, and predator density (e.g. Menshutkin et al. 1968) might expand the use of this model to examine the role of predation and cannibalism in regulating year-class strength. Unfortunately, sufficient data to support these model extensions is rarely available for any

single percid population. Data requirements include stock size, age distribution, recruitment, seasonal temperature regime at location of fish stock, spawning time and temperature, periods of occurrence of various development phases, specific food biomass, and predator density. While it might be said that the existence of such data sets would obviate the need for a model, this approach or a similar one proposed by Kipling (1976) may nevertheless aid future experimental design in sorting out causal relationships.

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ALM, G. 1951. Year class fluctuations and span of life of perch. Rep. Inst. Freshwater Res. Drottningholm 33: 17–38.

BAGENAL, T. B. 1977. Effects of fisheries on Eurasian perch (*Perca fluviatilis*) in Windermere. J. Fish. Res. Board Can. 34. (This issue)

BALON, E. K. 1975. Terminology of intervals in fish development. J. Fish. Res. Board Can. 32: 1663–1670.

BOIKO, E. G. 1964. Evaluation of the natural mortality of the Azov perch pike. Tr. Vses. Nauchno Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 50: 143–162.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26: 2363–2394.

BUSCH, W. N., R. L. SCHOLL, AND W. L. HARTMAN. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie 1960–70. J. Fish. Res. Board Can. 32: 1733–1743.

CARLANDER, K. D. 1977. Biomass, production, and yields of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in North American lakes. J. Fish. Res. Board Can. 34. (This issue)

CARLANDER, K. D., AND PAYNE. 1977. Year-class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with varied fry stocking rates. J. Fish. Res. Board Can. 34. (This issue)

CHEVALIER, J. R. 1977. Changes in walleye (*Stizostedion vitreum vitreum*) population in Rainy Lake and factors in abundance, 1924–75. J. Fish. Res. Board Can. 34. (This issue)

CLADY, M. D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. J. Fish. Res. Board Can. 33: 1887–1893.

CONOVER, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons, Inc., New York, N.Y. 462 p.

DERBACK, B. 1947. The adverse effect of cold weather upon the successful reproduction of pickerel, *Stizostedion vitreum*, at Hemming Lake, Manitoba, in 1947. Can. Fish Cult. 2: 22–23.

DOAN, K. H. 1942. Some meteorological and limnological conditions as factors in the abundance of certain fishes in Lake Erie. Ecol. Monogr. 12: 294–314.

EL-ZARKA, S. E.-D. 1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay, Lake Huron. U.S. Fish. Wildl. Serv. Fish. Bull. 151: 365–415.

ESHENRODER, R. L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34. (This issue)

FORNEY, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–73. J. Fish. Res. Board Can. 33: 783–792.

1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34. (This issue)

HARTMAN, W. L. 1972. Lake Erie: effects of exploitation, environmental changes and new species on the fishery resources. J. Fish. Res. Board Can. 29: 899–912.

HEYERDAHL, E. G., AND L. L. SMITH JR. 1971. Annual catch of yellow perch from Red Lakes, Minnesota, in relation to growth rate and fishing effort. Univ. Minn. Agric. Exp. Stn. Tech. Bull. 285: 4–51.

HOKANSON, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34. (This issue)

HOKANSON, K. E. F., AND C. F. KLEINER. 1974. Effects of constant and rising temperatures on survival and developmental rates of embryonic and larval yellow perch, *Perca flavescens* (Mitchill), p. 437–448. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, N.Y.

JOBES, F. W. 1952. Age, growth, and production of yellow perch in Lake Erie. U.S. Fish Wildl. Serv. Fish. Bull. 52: 205–266.

JOHNSON, F. H., AND J. G. HALE. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieui*) in four northeastern Minnesota lakes, 1948–69. J. Fish. Res. Board Can. 34. (This issue)

JOHNSON, F. H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. 34. (This issue)

JOHNSON, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459–2488.

JOHNSTON, D. A. 1977. Population dynamics of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in Lake St. Clair especially during 1970–76. J. Fish. Res. Board Can. 34. (This issue)

KELSO, J. R. M., AND F. J. WARD. 1977. Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. J. Fish. Res. Board Can. 34. (This issue)

KEMPINGER, J. J., AND R. F. CARLINE. 1977. Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin 1955–72. J. Fish. Res. Board Can. 34. (This issue)

KIPLING, C. 1976. Year-class strength of perch and pike in Windermere. Anim. Rep. F.B.A. 44: 68–75.

KITCHELL, J. F., J. F. KOONCE, R. V. O'NEILL, H. H. SHUGART JR., J. J. MAGNUSON, AND R. S. BOOTH. 1974. Model of fish biomass dynamics. Trans. Am. Fish. Soc. 103: 786–798.

KITCHELL, J. F., D. STEWART, AND D. WEININGER. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34. (This issue)

KUZNETSOV, V. A. 1970. Spawning grounds of some percid fishes in Sviyaga Bay, Kuybyshev Reservoir, the distribution of larvae and the effectiveness of reproduction. J. Ichthyol. Am. Fish. Soc. 10: 765–771.

LEACH, J. H., AND S. J. NEPSZY. 1976. The fish community in Lake Erie. J. Fish. Res. Board Can. 33: 622–638.

LIND, E. A. 1977. A review of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatalis*), and ruff (Gymnocephalus cernua) in Finland. J. Fish. Res. Board Can. 34. (This issue)

MCCORMICK, J. H. 1976. Temperature effects on young yellow perch, *Perca flavescens* (Mitchill). U.S. Environ. Prot. Agency, Ecol. Res. Ser. EPA-600/3-76-057: 18 p.

MENSHUTKIN, V. V., AND L. A. ZHAKOV. 1964. Mathematical determination of the nature of the population dynamics of perch in given ecological conditions, p. 140–154. *In* Ozera Karel; skogo Peresheika, Limnologiya i Metodika Issledovanii. Moscov. (In Russian)

MENSHUTKIN, V. V., L. A. ZHAKOV, AND A. A. UMNOV. 1968. A model method examination of causes of death among young perch. Prob. Ichthyol. Am. Fish. Soc. 8: 704–712.

MOMOT, W. T., J. ERICKSON, AND F. STEVENSON. 1977. Maintenance of a walleye, *Stizostedion vitreum vitreum*, fishery in a eutrophic reservoir. J. Fish. Res. Board Can. 34. (This issue)

NAGIĘĆ, M. 1977. Pikeperch (*Stizostedion lucioperca*) in its natural habitats in Poland. J. Fish. Res. Board Can. 34. (This issue)

NELSON, W. R., AND C. H. WALBURG. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River reservoirs. J. Fish. Res. Board Can. 34. (This issue)

OHIO DEPARTMENT OF NATURAL RESOURCES. 1961. Water temperatures at Put-in-Bay, Ohio from 1918. Ohio Dept. Nat. Resour. Tech. Rep. N-189: 36 p.

PAYNE, N. R. 1964. The life history of the walleye, *Stizostedion vitreum vitreum* (Mitchill) in the Bay of Quinte. M.A. Thesis. Univ. Toronto, Toronto, Ont. 40 p.

PRIEGEL, G. R. 1970. Reproduction and early life history of the walleye in the Lake Winnebago Region. Wis. Dep. Nat. Resour. Tech. Bull. 45: 1–105.

RUNDBERG, H. 1977. Trends in harvests of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and northern pike (*Esox lucius*) and associated environmental changes in lakes Mälaren and Hjälmaren 1914–74. J. Fish. Res. Board Can. 34. (This issue)

SCHNEIDER, J. C., AND J. H. LEACH. 1977. Walleye (*Stizostedion vitreum vitreum*) fluctuations in the Great Lakes and possible causes, 1800–1975. J. Fish. Res. Board Can. 34. (This issue)

SHUTER, B. J., AND J. F. KOONCE. 1977. A dynamic model of the western Lake Erie walleye (*Stizostedion vitreum vitreum*) population. J. Fish. Res. Board Can. 34. (This issue)

SMITH, L. L. JR. 1977. The walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations and fisheries of the Red Lakes, Minnesota, 1930–75. J. Fish. Res. Board Can. 34. (This issue)

SMITH, L. L. JR., AND L. W. KREFTING. 1953. Fluctuations in production and abundance of commercial species in the Red Lake, Minnesota, with special reference to changes in the walleye population. Trans. Am. Fish. Soc. 83: 131–160.

SPANGLER, G. R., N. R. PAYNE, AND G. K. WINTERTON. 1977. Percids in the Canadian waters of Lake Huron. J. Fish. Res. Board Can. 34. (This issue)

SUMARI, O. 1971. Structure of ther perch populations of some ponds in Finland. Ann. Zool. Fenn. 8: 406–421.

SVARDSON, G., AND G. MOLIN. 1973. The impact of climate on Scandinavian populations of the sander, *Stizostedion lucioperca*/L. Rep. Inst. Freshwater Res. Drottningholm 53: 112–139.

VIRBICKAS, J., A. GERLUAITIS, D. MISIVNIENE, and D. SINEICIENE. 1974. Biology and fishery of the pikeperch in the water bodies of Lithuania. State Publ. House MINTIS. VILNIUS. 276 p.

WILLEMSEN, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34. (This issue)

WALBURG, C. H. 1972. Some factors associated with fluctuation in year-class strength of sauger, Lewis and Clark Lake, South Dakota. Trans. Am. Fish. Soc. 101: 311–316.